

Mice, Land Bridges and Latin American Faunal Interchange¹

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REVIEW OF THE HISTORY OF SOUTH AMERICAN MAMMALS

The history of South American mammals begins with the Paleocene records from Argentina. The order Marsupialia is represented here by three superfamilies. The didelphoid opossums are known from abundant remains but the family Didelphidae was in North America since the Cretaceous. The carnivore-like borhyaenoids which compose the second superfamily were the principal predators of the South American Tertiary. Fossils of the third superfamily, the small shrew-like caenolestoids, are known from the Eocene of Argentina but species of this group were present in southeastern Brazil during the upper Paleocene. Remains of armadillos which were similar to living species of the edentate order Xenarthra appear in the Argentine Paleocene, while fossils of related glyptodonts, ground sloths, and anteaters, are of a later period in the Tertiary. Members of the extinct order of primitive ungulates, the Condylarthra, and five intimately related orders of peculiar South American hoofed animals had already attained a high level of diversity during the Paleocene. The Notoungulata radiated into animals ranging in size and appearance from the rhinoceros-like to the hare-like. The Litopterna evolved into forms resembling horses, camels, and small antelopes. Some of the Astrapotheria have been compared with rhinoceroses and hippopotami. Little is known of the Paleocene Xenungulata but the few recognized members of this order are among the oldest of South American mammals. The proboscidian-like Pyrotheria date from the Eocene and seem to have been the last of the native South American ungulates to evolve.

Precisely how and when these animals first arrived in South America is unknown. Except for marsupials and condylarths, there is no record of

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the occurrence of such animals in Middle America or northern South America prior to their appearance in southern South America.

Knowledge of what are presently regarded as later invasions is similarly deficient. Rodents of the suborder Caviomorpha appeared nearly full bloom in the Oligocene of the southern half of the continent. Their progenitors must have invaded South America earlier but none of the steps leading to the build-up has been discovered. Monkeys of an organization quite like that of living South American primates appeared as suddenly in the upper Oligocene of southern Patagonia. Nothing is known of their platyrrhine ancestry. There is no record of the evolution and dispersal of neotropical Primates from early Tertiary prosimians of the middle latitudes of North America to Oligocene ceboids of the middle latitudes of South America.

The next records of new faunal elements in the South American Tertiary date from middle or perhaps early Miocene with the appearance of the dolphin *Proinia* True, a genus supposedly of the family Susuidae (order Cetacea). Two genera of this family survive in South American waters with one, *Inia*, confined to fresh water. Whatever the systematic position of *Proinia* (cf. Kellogg, 1942) of the Patagonian marine deposits, the Pliocene *Ischyorhynchus* Ameghino is a true river susuid and very nearly related to *Inia*.

The La Venta fossils discovered in Central Colombia (cf. Stirton, 1953) give an inkling of the great variety and wide dissemination of South American mammals by late Miocene. They include remains of many of the southern forms already known and, in addition, fragments of true cebid monkeys, a bat of the family Phyllostomidae (Chiroptera), and a river manatee of the family Trichechidae (order Sirenia). Late Miocene or early Pliocene saw the arrival of members of the raccoon family, Procyonidae (order Carnivora). Finally in the upper Pliocene, mice of the murid subfamily Cricetinae (Myomorpha, order Rodentia) had already evolved into forms indistinguishable from representatives of living sigmodonts. Evidently, they thrived in great numbers on the plains of north-eastern Argentina together with herds of peccaries (Tayassuidae, order Artiodactyla) which had migrated from the north. Skunks of the family Mustelidae (order Carnivora) may also have invaded South America at this time but the oldest fossil, discovered in Eastern Buenos Aires, may be early Pleistocene rather than late Pliocene.

Thus, by the end of the Tertiary, fossil evidence reveals that South America was inhabited by three superfamilies of the order Marsupialia, two of which survive; five superfamilies of the order Xenarthra of which two are now extinct; six orders of ungulates, five native and none with living issue; two families of the order Primates; one family of Cetacea with a genus confined to fresh water; one family each of Chiroptera, Sirenia, Carnivora, and two suborders of Rodentia, the still flourishing Caviomorpha and Myomorpha. The oldest records of all but three of these taxa are from the southern half of the continent. The ancestors of all South American orders or families that originated in North America left no sign of their sojourn in Middle America. With exceptions noted, their first passage through northern South America is also unrecorded. It is practically cer-

tain that additional mammalian families either invaded or arose in northern South America during the Tertiary but disappeared without trace. Still others now living in South America almost certainly arrived or evolved there during the late Tertiary but for lack of fossil evidence may be incorrectly adjudged to be post-Tertiary invaders.

Bats may have been the dominant and most diversified of small South American mammals throughout the Tertiary but only one genus of Phyllostomidae is known from that period. The other endemic tropical American chiropteran families are the Noctilionidae, Desmodidae, Natalidae, Furipteridae, and Thyropteridae. They were members of a very ancient fauna but only fragments of some of these have been found in Pleistocene owl pellets. Squirrels (Sciuridae) undoubtedly invaded South America several times from the north. The ancestor of the pygmy squirrel, *Sciurillus*, may well have been the first to arrive, perhaps simultaneously with Middle Tertiary Primates. Successive invasions of dogs, mustelids, and deer may also have occurred but at a later date beginning perhaps with middle or late Pliocene. Tapirs of the order Perissodactyla are known from the Pleistocene but the first may have reached South America during late Pliocene. The same may apply to bears and cats which are also known from the Pleistocene of South America.

Horses and mastodons (order Proboscidea) arrived and disappeared during the Pleistocene but the camels survived.³ One genus of shrews, *Cryptotis* (Soricidae, Insectivora), one genus of rabbits, *Sylvilagus* (Leporidae, Lagomorpha) and one genus of spiny mouse, *Heteromys* (Heteromyidae, Rodentia) are among the latest arrivals and are representatives of the only other new mammalian families to invade South America since early Pleistocene.

MICE, MOVEMENTS AND BARRIERS

The advent of mice, or myomorph rodents, in South America is shrouded in mystery. A long history of differentiation in northern North America, Middle America, and South America preceded their appearance in the upper Pliocene of Argentina. Much of the evolution can be reconstructed from the morphology of living forms but the time of invasion and the routes of dispersal must be inferred from recent distributional patterns.

New World mice, the Cricetinae, are recorded from the Oligocene of North America but possibly arose in late Eocene. They may have originated in Eurasia and spread into northern North America, then Middle America and South America. Or, they may have arisen in northern North America and spread northward into the Old World and southward into South America. Insofar as the history of living cricetines is concerned, either hypothesis could be valid, but present knowledge favors the concept of a New World

³ The bovine *Colombibos ataetodontus* Hernandez Camacho and Porta, said to be from the upper Pleistocene of Colombia, is based, according to Thenius (1964, p. 275, footnote 4), on what seem to be the deciduous teeth of domestic cattle.

origin for cricetines. Whether the center was in northern or southern (*i. e.*, Middle American) latitudes of North America cannot be determined now. It is known that the most primitive of living cricetines are sylvan and the

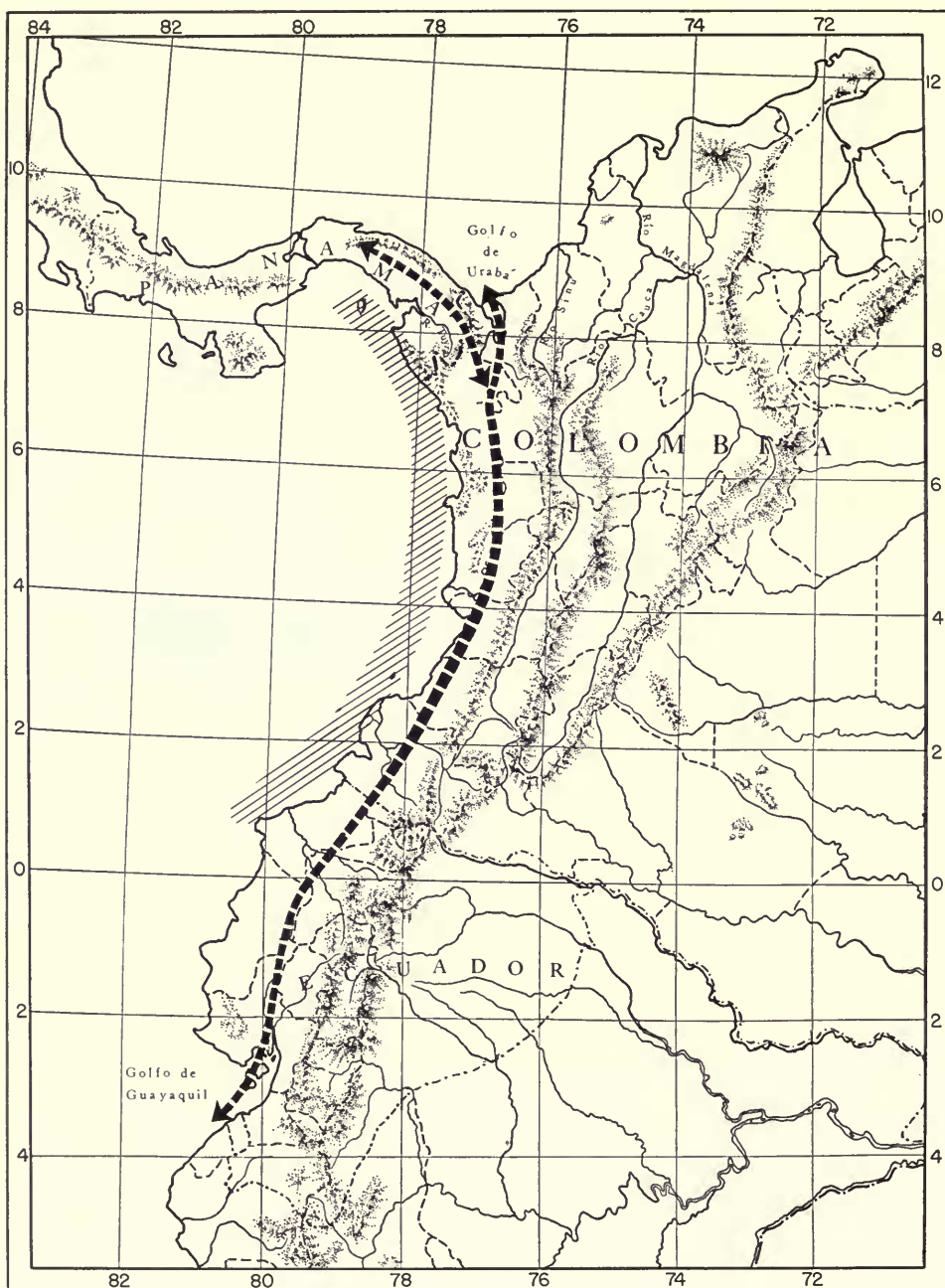


Fig. 151.—Axis of Bolívar syncline (bars) and western Tertiary borderland (diagonals) in Ecuador and Colombia with extension in Panamá. (Adapted from Nygren, 1950, fig. 1)

ancestral form must also have been sylvan with all the morphological characters distinguishing them from pastoral forms (cf. Hershkovitz, 1962, p. 16). Judged by the North American fossil record, it may be assumed that all well defined Recent genera of pastoral cricetines were already differentiated in the Pliocene.

Whatever its geological history during the Tertiary, Middle America must have served variously as a transition zone, a center of evolution and a staging area. From Middle America, cricetines and other New World mammals spread into higher northern latitudes in the wake of retreating glaciers and as suitable habitats became available. Their movements southward were largely controlled by geographic, tectonic, and ecological factors. Spread into South America was accomplished by means of over-water movements, *i. e.*, island hopping and waifing, by swimming or fording; or passively, by shifting land connections or cutoffs. It was finally accomplished via the Isthmian land bridge which only recently became complete at its South American terminal (fig. 152). Actual means or routes of dispersal used by the oldest migrants are hypothetical and need not have been the same or used at the same time by different individuals of the same species or different species.

A broad reconstruction of the history of mammalian faunas in Latin America has been presented by Simpson (1950). His account served as basis for orientation and has been universally accepted as an article of faith. I reproduce herewith the principal section (pp. 379-381) relating to the intercontinental exchange of faunas and the dissemination of cricetines in South America:

"A change like that going on in the Eocene on the World Continent also occurred in South America, but at a greatly later date, in the late Pliocene and Pleistocene . . . Its cause was the rise of the Central American bridge and the consequent irruption into South America of many derivatives from the fauna of the World Continent. This third broad faunal stratum did not come in all at once, in a single wave. Already in the late Miocene a few northern forms appeared, small arboreal placental carnivores more or less related to the raccoon. Not long thereafter, apparently in early Pliocene times, some South American animals, ground sloths, reached North America. These forerunners do not seem to indicate a continuous land connection but probably utilized the island chain, gaps in which were closing progressively as the Central American and northwestern South American regions rose relative to sea level. The exact moment when the bridge became complete is not established, but this probably occurred during the age called Chapadmalalan in South America and Blancan in North America, placed by some authorities as latest Pliocene and by others as earliest Pleistocene. Even then the exchange was at first rather limited in scope and the full surge of intermigration did not occur until somewhat later, in unequivocally Pleistocene times. Soon or late, at least fifteen (possibly sixteen) families invaded South America in this great episode . . .

"Invasion occurred in both directions. By a moderate tabulation, fifteen families of North American mammals then spread into South America and seven families spread in the reverse direction. The main migrants to the south were rabbits, squirrels, field mice, dogs, bears, raccoons, weasels, cats, mastodons, horses, tapirs, peccaries, camels, and deer, including in most of these cases some variety of related forms."

The spectacle of fifteen or sixteen North American families and seven

South American families awaiting the propitious moment "in unequivocally Pleistocene times" to cross the Panamanian bridge is dramatic. Viewed in the light of fossil records and what is known of the ecological preferences, habits, and vagility of the animals concerned, the stage seems real enough but the scene is less a product of fact than fancy.

The geological and mammalian history of the Americas indicates that the Isthmian water gap was much less effective in isolating faunas than the climatic barrier across northern México. For most mammals the water gap may not have been more than a minor obstacle and for some such as otters and other aquatic and subaquatic animals, an invitation. It was certainly not as much a deterrent as water barriers crossed by mammals in reaching the Antilles, the Galápagos, the Philippines, Australia, New Guinea, and other islands well off the continental shelves. Evidently, many northern families which spread through the Isthmus to the edge of the gap crossed it opportunely. Herds of wandering mastodons, tapirs, horses, pecaries, camels and deer would cross such bodies of water easily and routinely just as their living relatives do today. Island chains and rafts provided others with means of access to opposite shores. Unaquatic mammals such as ground sloths and related edentates were crossing the water gap since middle and probably early Pliocene while monkeys crossed at various times since the Oligocene or perhaps late Eocene. Despite the absence of fossil evidence, there is no reason to assume that many more families of contemporaneous mammals, some better adapted to water than others, were not doing the same. The traffic was both active and passive and from either continent to the other.

Rodents habitually crossed water barriers and colonized continental and oceanic islands throughout the world. Latin American cricetines are no exception. The vole-like terrestrial or pastoral species seem to have been even more successful than their aquatic relatives in crossing water barriers and ranging widely.

At the time of the Pliocene-Pleistocene transition when, according to Simpson's dictum, the intercontinental faunal exchange was about to begin, complex-penis-type genera and tribes of cricetines (see below) had already become differentiated in South America and reached nearly their present limits of natural dispersal in both North and South America. By late Pliocene, *Sigmodon*, the most generalized member of the South American sigmodont group, had invaded North America at least as far as Kansas (Hibbard, 1937, p. 247). At the southern extreme, late Pliocene *Proreithrodon* Ameghino (inseparable from Pleistocene *Ptyssophorus* Ameghino and *Tretomys* Ameghino and from Recent *Reithrodon* Waterhouse) was already one of the most common rodents of Patagonia (Hershkovitz, 1955, p. 639 ff.). Other Pleistocene cricetines of northeastern Argentina are also identical with living forms. The rich and well preserved fossil mammals of the Pleistocene of Minas Gerais, eastern Brazil, discovered in the first half of the last century by the Danish paleontologist Wilhelm Lund, are, for the most part, indistinguishable from living mammals of the same region.

Closure of the Panamanian portal may have facilitated the crossing of

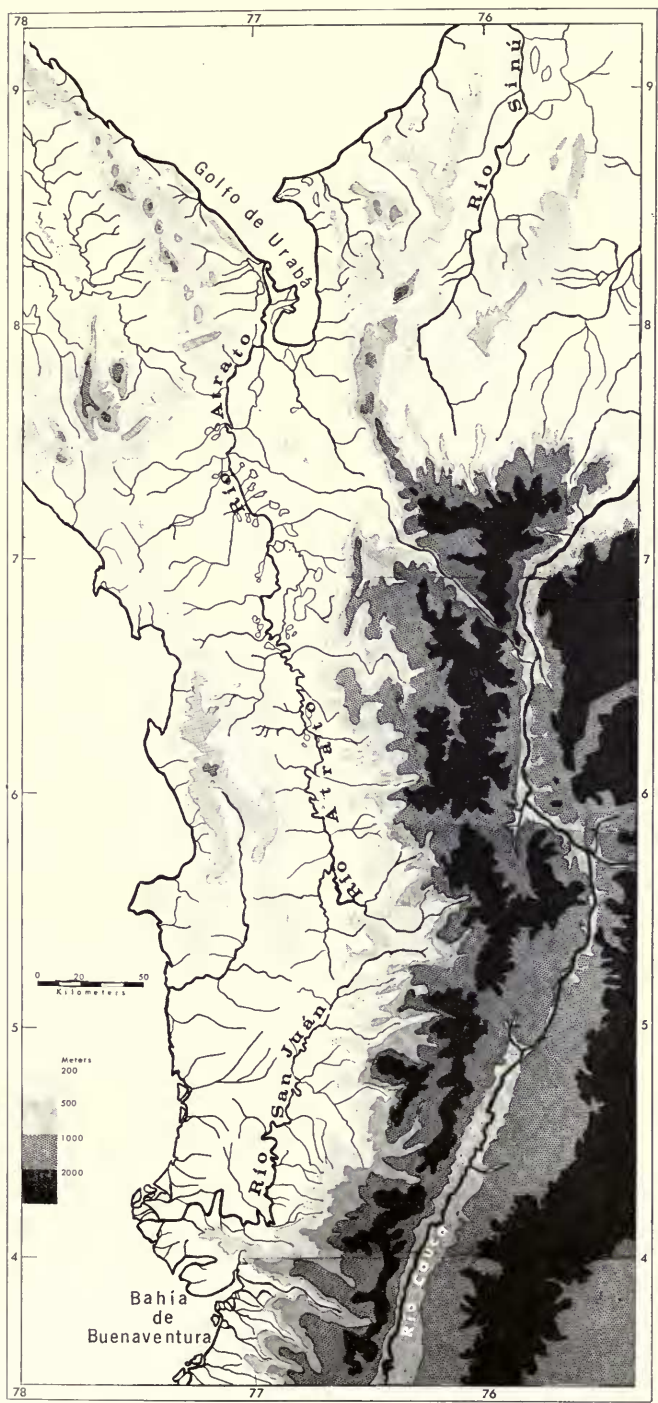


Fig. 152.—Río Atrato-Río San Juan basin, western Colombia. Land bridge connecting North and South America across the western border of the former Isthmian seaway is the *narrow divide* between the two rivers. The river channels follow the axis of the Bolívar geosyncline.

some species but there is no evidence that it resulted in a spectacular increase in the volume of faunal interchange.

THE CRICETINE GLANS PENIS IN TAXONOMY AND NEW WORLD ZOOGEOGRAPHY

New and Old World cricetines (Cricetinae) and microtines (Microtinae) are here treated as subfamilies of Muridae. This classification combines, in effect, all categories of the Muridae and Cricetidae of Simpson (1945, pp. 83, 205) or Wood (1955, p. 176) into the single family Muridae as recognized by Ellerman (1941, p. 1).

Recent studies of the glans penis and male accessory reproductive glands support this classification and add considerable data to our knowledge of the interrelationships of many of the species, genera and supergeneric assemblages of murids.

Two basic phallic types within the Muridae are demonstrated by Hooper (1958, 1959, 1960, 1962), Hooper and Hart (1962), Hooper and Musser (1964a, 1964b) and are discussed by Hershkovitz (1966).

The first or complex penis type (fig. 153A) is characterized by a baculum with typically three terminal digits and paired sac-like sinuses of the spongy tissue of the glans. This type predominates in Old World and South American Cricetinae, Murinae, Gerbillinae, Microtinae, and probably others including otomyines and dendromurines. The simple type penis (fig. 153B) is distinguished by the absence of lateral bacular digits and sacculations in the spongy vascular layer of the glans. It characterizes the essentially Holarctic peromyscine Cricetinae comprising the thirteen genera, *Peromyscus*, *Reithrodontomys*, *Aporodon*, *Onychomys*, *Baiomys*, *Scotinomys*, *Ochrotomys*, *Neotomodon*, *Nelsonia*, *Ototylomys*, *Tylomys*, *Neotoma*, and *Xenomys*.

Complex and simple phallic types are not restricted to murids and the simple type is not confined to peromyscines. Hooper and Musser (1964a) demonstrate simple or intermediate phallic types among some Old World cricetines (*Myospalax*, *Mystromys*), South American cricetines (*Nyctomys*, *Otonyctomys*, *Scapteromys*), nesomyines (*Macrotrarsomys*) and microtines (*Dicrostonyx*), some species of *Microtus*, *Ellobius* (cf. Hooper and Hart, 1962). Hooper and Musser (1964a, p. 53) also mention a simple type penis among murines but do not identify the species.

The simple penis is derived from the complex and arose independently in all major murid categories (cf. Hershkovitz, 1966). Simplification may be effected by reduction and elimination of the lateral bacular digits, as has occurred in all peromyscines, some murines (Bittera, 1918, p. 414), some microtines (Hooper and Hart, 1962), and some South American cricetines (Hooper and Musser, 1964a; Hershkovitz, 1966). It may also result from reduction and elimination of the middle digit only, as in the South American *Scapteromys*, *Phyllotis*, and *Zygodontomys* (Hershkovitz, 1966); or by fusion of all digits, as in most *Scapteromys* (Hershkovitz, 1966).

Members of the peromyscine group are a diverse lot judged by external, cranial, and dental characters. The penis, although of the simple type is

also highly diversified within the group. Hooper and Musser (1964a) divide peromyscines into two groups. Earlier, Hooper (1960) had arranged them in four. The several convergent paths leading to a simple penis increase the probability that peromyscines are polyphyletic. In any case, it is virtually certain that peromyscines, individually or collectively, are derived from the same complex penis type stock now represented by South American cricetines. These two assemblages, the essentially North American

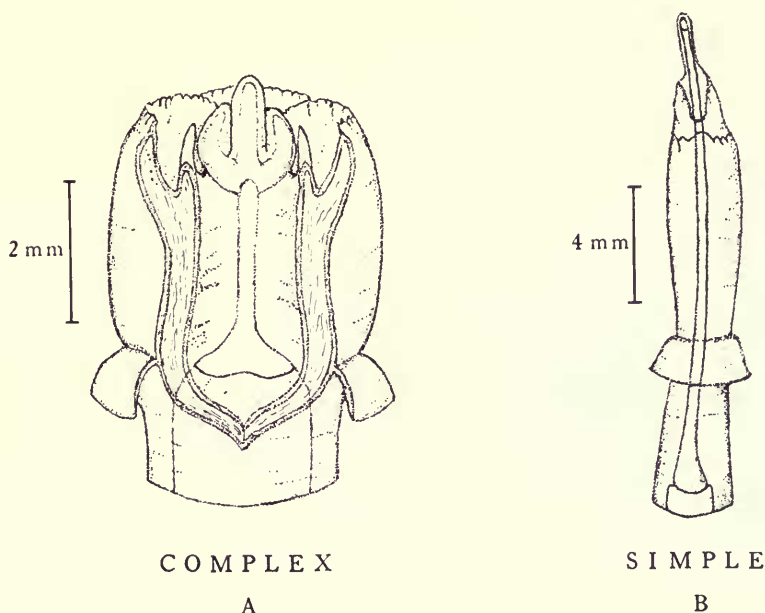


Fig. 153.—Glans penis of New World cricetines. A, complex type with three digitate baculum in *Oryzomys flavescens* (after Hooper, and Musser, 1964a, fig. 1h). Glans of A dissected midventrally to expose baculum. B, simple type with simple rod-like baculum in *Peromyscus pirrensis* (after Hooper and Musser, 1964b, fig. 1e). Glandes cleared and stained to reveal internal structures.

peromyscines with simple penis and the essentially South American cricetines with complex penis, are the primary indicators of inter-American exchanges of mammalian faunas during the late Cenozoic. Their separate dispersal patterns form a mosaic of five faunal strata.

Old North and Middle American cricetines, representing stratum I (fig. 154) migrated over water, i. e., by island hopping or waifing, into South America and radiated there into representatives of stratum II. Descendants of some elements of stratum II returned by over water routes to Middle America and differentiated significantly forming stratum III. Finally, late migrants of South American stock spread over the completed Isthmian land bridge and are identified as stratum IV. North American elements also spread at the same time by the same route into South America and be-

came stratum V. There has been little or no change in the taxonomic grade of either stratum IV or V.

Many mammals and other vertebrates belong to the same faunal strata as the cricetines. The following section, however, describes the five strata in terms of cricetines only.

LATIN AMERICAN CRICETINE FAUNAL STRATA

STRATUM I. OLD MIDDLE AMERICAN COMPLEX PENIS TYPES.

Old complex penis types; evolved in situ or migrated from northern North America (fig. 154).

The only Middle American members of this stratum are the following two closely related monotypic genera,

Nyctomys

Otonyctomys

These are possibly relicts of the archaic North or Middle American stock from which the complex-penis-type thomasmomyines may be derived on the one hand, and from which the simple-penis-type peromyscines diverged on the other. The male genital tract and the accessory reproductive glands (Arata, 1964, p. 14) of *Nyctomys sumichrasti* and *Otonyctomys hatti* are reduced or simplified and approach those of peromyscines. Otherwise, they most nearly resemble species of the South American genera *Thomasomys* and *Rhipidomys*. The possibility that the stem form of *Nyctomys* and *Otonyctomys* evolved in South America and migrated over water into Middle America (see stratum II) must also be considered.

The Tertiary history of Middle American cricetines is unknown. There is no suggestion that *Eumys* of northern North American Oligocene may be ancestral. According to Clark, Dawson and Wood (1964, p. 42) some element of the *Eumys* complex may have given rise to "hesperomyines." Their phylogenetic chart (op. cit., fig. 5) shows a line leading to *Leidymys* (Oligocene-early Miocene) through *Copemys* (late Miocene-early Pliocene) to *Peromyscus* (upper Pliocene and later). Another branch leads from *Leidymys* to *Miochomys* (late Miocene) then directly to *Onychomys* of the same horizons as *Peromyscus*. It seems that the "hesperomyines" of these authors equals the peromyscines of neomammalogists. The name peromyscine, or the tribal form Peromyscini, is zoologically correct and nomenclatorially valid for North American simple-penis-type cricetines (see nomenclatorial note p. 746).

STRATUM II. SOUTH AMERICAN COMPLEX PENIS TYPES.

Descendants of stratum I; migrated over water from Middle America into South America (fig. 154); evolution to generic and tribal grades.

There are approximately 50 genera and 300 species of South American cricetines. Samplings of a large number of genera (cf. Hooper and Musser, 1964a) show all to be of the complex penis type. The affinities of the remaining genera are such as to virtually preclude the possibility that any of them are not of the same basic type. Ancestral species arrived in South America during the Tertiary, perhaps from Miocene onward. Subsequent intercontinental movements of complex-penis-type cricetines may have been, until late Pliocene-Pleistocene, almost entirely from South America into North America (see strata III and IV, beyond).

Fossil cricetines congeneric with living South American forms are known from the Pleistocene of southeastern Brazil and the late Pliocene and Pleistocene of northeastern Argentina. There is no likelihood that the evolution of the more highly specialized and geographically restricted species and generic clusters could have taken place anywhere else than *in situ*. The evolution of most of these forms can be reconstructed from the extant South American fauna.

For a discussion of the adaptive radiation, dispersal, and taxonomy of some of the genera and generic groups see Hershkovitz (1944, 1955, 1960, 1962, 1966).

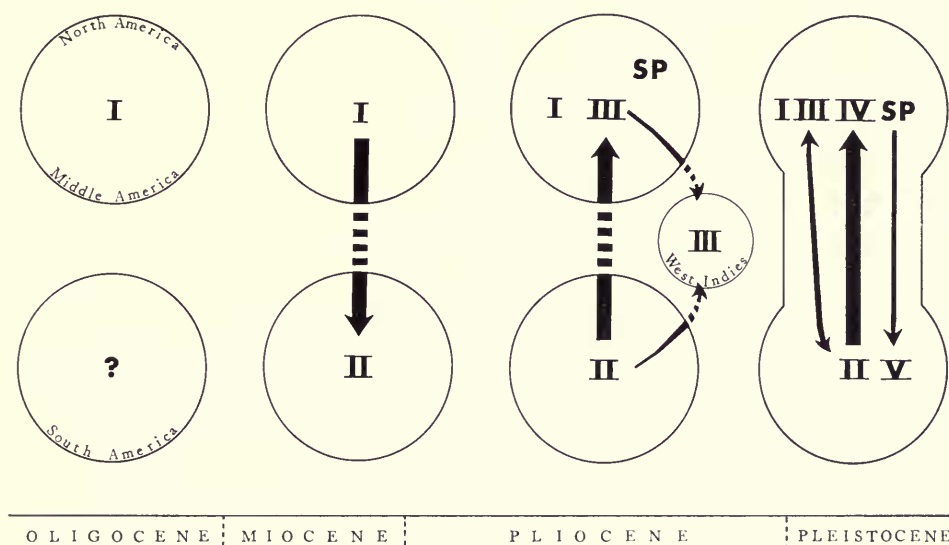


Fig. 154.—Cricetine rodent faunal strata (Roman numerals) in Middle and South America. Broken arrows indicate over water migration, solid arrows over land. Stratum I = old North American complex-penis-type mice. Stratum II = tribes and genera of South American complex-penis-type mice evolved from I. Stratum III = genera and species of Middle American and West Indian complex-penis-type mice differentiated from II. Stratum IV = slightly differentiated Middle American descendants of II. SP = North American simple-penis-type mice. Stratum V = slightly differentiated simple-penis-type migrants in South America.

STRATUM III. OLD SOUTH AMERICAN MIGRANTS IN NORTH AMERICA.

Early descendants of stratum II; migrated over water into Middle America and the West Indies (fig. 154); evolution to species and generic grades.

Three genera, *Sigmodon*, *Oryzomys* and the extinct oryzomyine genus *Megalomys* compose this stratum. They are of the complex penis type and derived from South American stock. *Sigmodon* is represented by several extinct and living species, all closely related and treated here as a single species complex with an intricate geographic history. The genus *Oryzomys*

of this stratum includes ten species, one extinct, and two subgenera including the nominate form. The West Indian *Megalomys* is known from the Pleistocene and the Recent but was exterminated in historic time. Remains of one species have been found near those of ground sloths. The North American migrations of *Oryzomys* and *Sigmodon* also coincided largely with the movements of ground sloths, glyptodonts and giant armadillos.

The species groups of *Sigmodon* and *Oryzomys* are listed below in the order of the magnitude of their geographic range from north to south.

Sigmodon hispidus complex

The North American range of *Sigmodon* is greater than that of any other complex-penis-type cricetine. Its present and past distribution in North America points to the cotton rat as one of the earliest over-water migrants from South America. It has been recorded from the upper Pliocene of Kansas (*S. intermedius* Hibbard, 1937, p. 247) and *S. hispidus* was in Florida during Pleistocene. Successive invasions from South America, or reinvasions of South America from Middle America, may account for the continuous distribution of living *Sigmodon hispidus* in Middle and northern South America.

The extinct species of North American *Sigmodon* are properly components of strata III. On the other hand, Recent and Pleistocene *S. hispidus* may be a late arrival and an element of strata IV. The equal if not greater probability is, however, that *Sigmodon hispidus* has been a persistent and pervasive element in all faunas from strata II to V.

The sigmodont upper right molar described but not named by Black (1963, p. 485) from the early Miocene Thomas Farm locality in Gilchrist County, Florida, is tantalizing. The enamel pattern of the tooth most nearly resembles that of *Sigmodon*. The occlusal surface, however, is said to be terraced. The molars of *Sigmodon* are plane, hence more specialized. The Thomas Farm tooth may represent a true sigmodont, a parallel development or, less likely, an extinct side issue of the *Eumys*-peromyscine line.

Oryzomys palustris complex

palustris (= *couesi*, *azuereensis*, *cozumelae*, *gatunensis*, *antillarum*)

Fossils identified as *O. palustris* are known from the Pleistocene (Illinoian?) of Florida (Gut and Ray, 1963, p. 325). Examination of the type of *Oryzomys antillarum* Thomas from Jamaica shows it to be a weakly differentiated member of the *palustris* group. It may be treated as a subspecies, *Oryzomys palustris antillarum* Thomas. In reaching Jamaica as a waif it crossed a much wider water gap than any separating the Americas at the Isthmus during the Tertiary.

peninsulæ

fulgens

nelsoni

fossilis (extinct)

Described by Hibbard (1955, p. 213) from the Pleistocene interglacial (Sangamon?) of Meade County, southwestern Kansas. The genus *Oryzomys* does not exist in Kansas now, but Hall (1955, p. 246) notes a specimen of *O. palustris* in the U. S. National Museum said to have been collected in Neosho Falls, southeastern Kansas, by B. F. Goss, in 1859.

Oryzomys melanotis

If this proves to be a member of the *O. alfaroi* group it belongs in faunal stratum IV (below). Subgeneric affinities undetermined.

Oryzomys bombycinus

Subgeneric affinities undetermined but near *O. melanotis*.

Oryzomys aphaestus

Known from the type specimen only, a skin with shattered skull. Its nearness to

Nectomys (Sigmodontomys) alfari suggests that *aphrastus* might belong to faunal stratum IV.

Oryzomys (Micronectomys) dimidiatus

Micronectomys is known from the type specimen only. Should representatives of *O. dimidiatus* be discovered in South America it would be treated as a member of faunal stratum IV.⁴

With the possible exceptions noted, the degree of divergence of the Middle American species of *Oryzomys* from their South American stems implies a long isolation. The morphological differences suggest polyphylety and their geographic distribution indicates successive invasions. Members of the *O. palustris* complex have spread farthest north and are the most differentiated from South American species. They are known from the Pleistocene of southern and central United States. The more southern species of *Oryzomys* are more closely related to their South American relatives.

Megalomys curazensis

Described by Hooijer (1959) from the late Pleistocene of Curaçao. It was contemporaneous with *Paulocnus* Hooijer (1962), a megalonychid ground sloth.

Megalomys desmarestii

Known from the Lesser Antillean islands of Martinique, Santa Lucia and Barbuda (Pleistocene). The species has been exterminated. Its nearest living relative appears to be the scansorial *Oryzomys (Macruroryzomys) hammondi* of northwestern Ecuador.

Oryzomys pliocaenicus Hibbard (1939:539) from the Edson Quarry Pliocene of Kansas is not an *Oryzomys* according to Hibbard (*in litt.*). Dr. Hibbard adds that he re-examined the type in 1952 and believes it may prove to be a species of *Bensonomys* Gazin.

Eligmodontia arizonae Gidley, 1922, from the San Pedro Valley Pliocene in Arizona, was made type of the genus *Bensonomys* by Gazin (1943, p. 489). It has nothing to do with *Eligmodontia* Waterhouse, a genus of gerbil-like mice of the southern half of South America.⁵

STRATUM IV. LATE SOUTH AMERICAN MIGRANTS IN MIDDLE AMERICA

Late descendants of stratum II; spread over Panamanian land bridge into Middle America (fig. 154); low grade subspeciation.

Thirteen complex-penis-type species representing seven cricetine genera are common to North and South America. Their geographic and genetic continuity can be traced across the Panamanian land bridge.

Sigmodon hispidus

Zygodontomys brevicauda (see Hershkovitz, 1962:203, for taxonomy)

Rhipidomys scandens (genus unrevised and Colombian representative of *scandens* not presently determined)

Nectomys alfari

⁴"*Oryzomys (Micronectomys) borroeroi*" Hernández, from the Río Chucuri Valley, Santander, Colombia, is undoubtedly an *Oryzomys* but, judged by the original description, it is certainly not a *Micronectomys*.

⁵Simpson (1945, p. 84) overlooked the Gazin revision and includes "*Eligmodontia*" in the upper Pliocene fauna of North America.

Neacomys tenuipes (includes *pictus*)

Rheomys trichotis (includes *thomasi*, *underwoodi*, *hartmanni* and *raptor*)

Oryzomys alfaroi

Oryzomys capito (= *talamancae*)

Oryzomys albigularis (= *devius*, *pirrensis*)

Oryzomys concolor (= *tectus*)

Oryzomys bicolor (= *endersi*, *trabeatus*)

Oryzomys caliginosus

Oryzomys nigripes complex (subgenus *Oligoryzomys*; includes *fulvescens*, *delicatus*, *victus*, *longicaudatus*, *delticola* and others)

Of the species listed above, only *Sigmodon hispidus* has a range extending north of the Middle American province. Its distribution through faunal strata II-IV inclusive, is discussed in the preceding section. The vole-like *Sigmodon* and *Zygodontomys* are true pastoral forms. The ichthyomine *Rheomys trichotis* is also derived from a pastoral stock but is highly specialized for aquatic life and fish eating. The remaining species are sylvan. *Rhipidomys* is arboreal, *Nectomys* subaquatic, *Neacomys* terrestrial and the species of *Oryzomys* vary from strictly terrestrial (*O. albigularis* and the vole-like *O. caliginosus*) to the arboreal *O. concolor*. Members of the unrevised *Oryzomys nigripes* complex range from southern México to the straits of Magellan. They are terrestrial and scansorial and live in forests, woodlands, bordering fields and open savannas from sea level to above tree line in the Andes. *Oryzomys victus* Thomas, from Saint Vincent, Lesser Antilles, is a well differentiated *Oligoryzomys*, geographically nearest *O. delicatus* of Trinidad. Unless recently imported, it represents faunal stratum IV in the West Indies.

Faunal flow of stratum IV from South America to North America via the Isthmian land bridge seems to have been greater in volume and richer in variety than the flow of stratum V in the opposite direction.

STRATUM V. LATE MIDDLE AMERICAN MIGRANTS IN SOUTH AMERICA

Late descendants of North American simple penis types (peromyscines); spread over Panamanian land bridge into South America contemporaneously with IV (fig. 154); low grade subspeciation.

The thirteen (to sixteen) recognized genera of autochthonous North American cricetines, not including *Nyctomys* and *Otonyctomys* (see stratum I, above), are peromyscines. They are characterized by a simple penis and include about 150 species. The geographic range of each of seven of the genera, namely, *Tylomys*, *Ototylomys*, *Aporodon*, *Reithrodontomys*, *Peromyscus*, *Scotinomys*, and *Neotoma*, extends into or is restricted to Middle America. Most of the fifty to sixty species assigned to these seven genera in Middle America are unrevised. Only the following two reached South America.

Tylomys nudicaudatus (includes *gymnurus*, *panamensis*, *watsoni*, *tumbalensis*)

Aporodon mexicanus

The two species are scansorial, the first frankly arboreal. Both range into the Andes of Colombia and northern Ecuador, and neither is more than subspecifically differentiated from its nearest Middle American relative. As in the case of the contemporaneous species of stratum IV (above), the geographic and genetic continuity between Middle and South American representatives of these species point to the land bridge migration route.

Peromyscus pirrensis Goldman appears to be a relict species confined to the Panamanian side of the Serranía del Darién. Hall and Kelson (1959, p. 653, map 374) indicate without documentation that the species occurs on the eastern or Colombian side of the Serranía.

Absence of simple-penis-type cricetines in South America except for the two recent invaders proves conclusively that this group originated in North America, perhaps in México.

As compared with Tertiary over water crossings, faunal flow across the Isthmian bridge from North America into South America was anticlimactic.

WATER GAPS, BRIDGES, AND TERTIARY FAUNAL INTERCHANGE

The American continents during Tertiary were at times connected, at others separated, by a waterway or a complex of islands and straits. The final and crucial barrier separating the faunas of Middle America and South America was the Bolívar geosyncline (fig. 151). According to Nygren (1950:1998, abstract):

"the Bolivar geosyncline extends through coastal Ecuador and Colombia from southwestern Ecuador to the Golfo de Uraba. Six cross-basin highs separate the deeps within the trough. Marine sedimentation began in the south in the middle Eocene, gradually encroached northward, and continued intermittently on into the upper Miocene. Several unconformities of varying importance are present. Post-Miocene sedimentation is mostly non-marine. During the early Tertiary the sediments were largely derived from the west, but after the lower Miocene they were mostly from the east. *Migration of terrestrial animals could have taken place through this area during the periods from upper Cretaceous to middle Eocene, middle Oligocene, lower Miocene, middle Miocene, and from upper Miocene to Recent* [italics mine]."

The western borderland of the Bolívar geosyncline is described by Nygren (p. 2005) as being a

"rather wide lowland area up until upper Middle Miocene [when it] was submerged by down-faulting . . . except for a little narrow strip of land close to the present coast line. Remnants such as submerged peaks near Esmeraldas, Ecuador, Gorgona Island, and peaks at Cabo Corrientes still remain . . . The eastern borderland was an area of low relief with embayments extending to the Cauca Valley in upper Oligocene time."

During middle Miocene, the

"eastern borderland was raised into the high peaks of the western Cordillera [op. cit. p. 2003]."

The north-south flowing Ríos Atrato and San Juan now drain the Colombian or Chocóan portion of the main axis of the Bolívar Trough (fig. 152). The Atrato empties into the Golfo de Urabá in the Caribbean and the San Juan flows into the Bahía de Buenaventura in the Pacific. Except for the low, narrow divide between their heads, *the Ríos Atrato-San Juan now constitute the last water barrier separating Middle and South American mammals.*

As the channels of the Atrato-San Juan became increasingly narrower through sedimentation more animals succeeded in crossing by ferrying, swimming or fording. As the meanders of the rivers became more numerous and sharper, more frequent cutoffs resulted and more habitats with their occupants passed from one side of the water gap to the other. Notwithstanding the accelerated rate of exchange, the mammalian fauna of the west

bank of the Atrato-San Juan is still predominantly Middle American and the entire coast from the Caribbean Golfo de Urabá in Colombia to the Pacific Golfo de Guayas in Ecuador is zoogeographically an integral part of the Middle American Province (Hershkovitz, 1958, p. 596).

The western or Middle American end of the Isthmian region was probably undergoing comparable changes in geomorphology. There may have been one or several successive straits across the Isthmus of Panama (cf. Lloyd, 1963, p. 88; Fischer and Pessagno, 1965, p. 433). Tertiary mammals on any part of the shifting intercontinental region were, in effect, straddling the two continents. Sooner or later some became established on the mainland of the opposite continent while others retreated or disappeared entirely. By the time the continents were welded in fact, all mammalian interchanges as we know them today on the generic level, and many of them on the specific level, had already been consummated.

LATE PLIOCENE-PLEISTOCENE FAUNAL INTERCHANGE

Precise dating of complete closure of the Isthmian water gap would necessarily be arbitrary and as far as mammalian zoogeography is concerned hardly more than academic. Nevertheless, this date has been a major concern of students of the interrelationships of continental faunas and its determination by Simpson as the period of transition from upper Pliocene to Pleistocene governed the thinking of all zoogeographers. Simpson's (1940, p. 694) reasons are expressed in the following quotation:

"In the Chapadmalalan [southeastern Buenos Aires Province, Argentina] for the first time many mammals of North American origin appear. They have inevitably undergone some change in the long journey but most or all of them could be derived from middle Pliocene forms in North America. These were the first animals surely to use the bridge. In North America animals of South American origin appear very sparingly in the middle Pliocene, then in more variety in the late Pliocene (Blancan stage). The middle Pliocene immigrants in North America are only a very few small ground sloths which could well have crossed (as did the procyonids in the reverse direction) before the bridge was quite complete and passable for the bulk of the fauna.¹² It was thus complete and passable by Blancan in the North American sequence and by Chapadmalalan in the South American. The evidence is strong for the approximate equivalence of Blancan and Chapadmalalan. The Blancan is now considered the typical late Pliocene in North America."¹³ [Footnote 13 follows:] "Some students insist that the earliest beds with any immigrant forms in the two continents should be synchronized, sometimes calling the Chapadmalalan middle Pliocene on this basis. Such a criterion, however, would make the Mesopotamian, not the Chapadmalalan, middle Pliocene, a correlation that is extremely improbable. It is more reasonable and more consistent with all other data to admit that the early stragglers crossed before the bridge was complete and to base synchronization on the beginning of extensive faunal interchange, a point already emphasized by Patterson (1937)."

The point emphasized by Patterson (1937, p. 379) in his abstract of an unpublished paper is that:

"it has generally been assumed that the Americas were reconnected about the beginning of the Pliocene. The vertebrates appear to oppose this view. Apart from raccoons and didelphines, no northern forms occur in the south until the end of the Pliocene, when a whole immigrant fauna suddenly appears. It is therefore held that the reconnection occurred in late middle Pliocene time at the earliest. Had it occurred earlier a more gradual diffusion southward of northern invaders

should be recorded. The didelphines and raccoons, and the megalonychine sloths found in the Middle Pliocene of North America are regarded as "waif" immigrants [i. e. over water]."

Patterson offers no evidence, but his sources are evidently the same used in Simpson's revision of the mammal-bearing Tertiary of South America. In this work, Simpson (1940, pp. 678-680) names seven families of North American origin in the Chapadmalalan but does not enumerate the Blancan migrants from South America. Stirton (1936, p. 172) whose correlation of North American Pliocene faunas was the consensus for the time, lists an unidentified ground sloth and a glyptodon (*Glyptotherium*) in the Blancan. The only other South American mammals included by Stirton in upper Pliocene are the cricetine *Sigmodon*, a genus then regarded as of North American origin, and the dubious "*Eligmodontia*" (= *Bensonomys*) of supposed South American origin (see p. 737). Regarding the Blancan ground sloth, Simpson (supra cit., p. 694, footnote 12) suggests it was "ancestral to or belonged to *Megalonyx*, a genus that arose in North America from primitive South American ancestors of Miocene or early Pliocene type." The Blancan glyptodont, so far as known, is also North American and therefore may have evolved from an earlier South American migrant. The Benson and Curtis Ranch *Sigmodon* remains as the only undoubted South American immigrant found in the North American late Pliocene. It is intimately related to the Chapadmalalan *Reithrodon*.

The seven Chapadmalalan families treated by Simpson as North American may have originated in North America or Eurasia. Only the history or place of origin of their South American representatives is relevant. These families and five Pampean (Pleistocene) families as listed by Simpson (1940, pp. 678-680), are enumerated as follows and then discussed separately.

- Cricetidae (mice)
- Procyonidae (raccoons, coatis, etc.)
- Ursidae (bears)
- Felidae (cats)
- Equidae (horses)
- Tayassuidae (peccaries)
- Cervidae (deer)

The following are listed as Pampean or Pleistocene.

- Canidae (dogs)
- Mustelidae (weasels, otters, etc.)
- Tapiridae (tapirs)
- Camelidae (llamas, vicuñas)
- Gomphotheriidae (mastodons)

The only Cricetidae, more precisely, Cricetinae, known from the Chapadmalalan is *Reithrodon*, an autochthonous mouse of the sigmodont group (see above p. 736). Cricetines ancestral to South American forms diverged from North American stock, possibly in the Oligocene. The initial invasion of South America was probably over water, and judged by the diversity and complexity of subsequent radiations and the pervasiveness of the dispersal may have occurred during early Pliocene or Miocene.

According to Reig (1958, p. 252), the Ursidae and Felidae are not Chapadmalalan. So far as known, South American bears and cats date from the Pleistocene and were subsequently so listed by Simpson (1945, pp. 111, 118).

Two extinct genera of Procyonidae found in the Chapadmalalan are known since Mesopotamian or early Pliocene. This old American family of carnivores may have originated and radiated in Middle America. In any case a distinct species of the nominate genus *Procyon* evolved in South America and two highly specialized and monotypic genera, the prehensile tailed kinkajou (*Potos*) and the olingo (*Bassaricyon*) are certainly tropical American if not specifically South American in origin. Fossil remains of these strictly arboreal animals are unknown.

Simpson had no knowledge of the occurrence of mustelids in the Chapadmalalan but Reig (1958, p. 252) records a species of hog-nosed skunk, *Conepatus*.⁶ The Mustelidae are cosmopolitan and well represented in South America. The respective histories of such recent South American mustelids as the giant Amazonian otter (*Pteronura*), the huron (*Lyncodon*) and the grisonella (*Grissonella*) as well as the skunk (*Conepatus*) must reach far back. *Mustela frenata* and *Lutra canadensis* (= *annectens*) are the only certain land bridge migrants from North America corresponding to cricetine stratum V. Whether the tayra (*Eira barbara*) and the grison (*Galictis vittatus*) spread from South to Middle America (stratum IV) or vice versa (stratum V), is moot. In any case, the dispersal of mustelids, particularly of otters, could not have been significantly controlled by minor water gaps.

Absence of canids from the Chapadmalalan or earlier formations may be misleading. The South American radiation of the Canidae culminated in several genera and more living species than evolved on any other continent. Such canids as *Chrysocyon*, *Atelocynus* and *Speothos* are most highly specialized for particular habitats in South America. The evolutionary history of these dogs is undoubtedly spread over a long span of time but the remains of their forest dwelling ancestors may be lost forever in middle Tertiary formations of tropical America. Among living canids,

⁶ There is some confusion attending the stratigraphic position of *Conepatus altiramus* Reig. It was first (1952, p. 45) said to be from lower Chapadmalalan in the Barranca de los Lobos region. Later Reig (1957, p. 39, footnote 3) reassigned it to the Barranca de los Lobos horizon which is lower Pleistocene. He then changed his mind again (1958, p. 252, footnote) and returned it to the Chapadmalalan on the basis of a personal inspection of the actual site of discovery shown him by the collector of the type specimen. Now, Churcher and Van Zyll de Jong (1965, p. 3) compound the confusion by omitting the distinction between Barranca de los Lobos as a geographic region and as a geological horizon and, without consulting the pertinent literature (cited above, see also Kraglievich, 1952) imply that *Conepatus altiramus* is of lower Pleistocene age. Apart from all this, there are grounds for questioning the occurrence of *Conepatus* in the upper Pliocene of Argentina. The genus was abundant in the Pleistocene and is common throughout South and Middle America today. Scores of "species" have been described but all appear to belong to the same species complex for which the oldest name available is *Conepatus chinga* Molina, 1782.

only the gray fox (*Urocyon*) is an undoubted late or land bridge migrant from Middle America and almost certainly belongs to the cricetine stratum V. The dire wolf *Aenocyon* Merriam, first known from the upper Pleistocene of North America, also appears in the upper Pleistocene of Talara, northwestern Peru (Lesson and Churcher, 1961, pp. 425-426). Like many others of the same faunal stratum it became extinct with the change from a moist to dry climate.

Peccaries are retained by Reig (op. cit., p. 246) in upper Pliocene but the form known to Simpson (*Antaodon chapalmalensis* Ameghino) is excluded. Horses and deer are also excluded. Later, Simpson (1945, pp. 137, 154) recorded the Equidae and Cervidae from the Pleistocene but not the Pliocene of South America. In any case, there is reason to believe that deer, at least, invaded South America during late Tertiary.

The history of the Cervidae parallels that of the Cricetinae. The forest-dwelling spike-antlered pudus and brockets are probably old over-water invaders; the more specialized woodland and savanna branch-antlered deer arrived later. The white-tailed deer, *Odocoileus virginianus*, with a continuous range from southern Canada to the northern half of South America, may have spread from Middle to South America over the completed land bridge (stratum V). One species of brocket (*Mazama americana*) returned over the same route to Middle America (stratum IV).⁷

Three species of tapirs occur in tropical America. The Andean *Tapirus pinchaque* and the lowland *T. terrestris* are confined to forested South America and certainly could have reached that continent by the over water route. *Tapirus bairdi* with a continuous distribution in Middle America and northwestern South America is evidently a late overland arrival and corresponds to cricetine stratum V. In spite of its vagility and aquatic proclivities, Baird's tapir seems to have crossed the Ríos Atrato-San Juan "gap" comparatively recently. So far as known, it has yet to reach the next important water gap, the Río Cauca-Magdalena, only some 100 kilometers distant across the lowlands (HersHKovitz, 1954).

From the foregoing it appears that only one genus of undoubted South American origin, the cricetine cotton rat *Sigmodon*, occurred in the upper Pliocene of North America. Of seven families of North American (and or Eurasian) origin treated by Simpson as Chapadmalalan in the upper Pliocene of South America, only three belong with certainty to that formation. Among their genera, the taxonomic units used here for correlations, only a peccary (*Platygonus*, Tayassuidae) may be of North American origin. All other undoubted Chapadmalalan genera originated in South America.

⁷ The Yucatán Península brocket is a red brocket and should be known as *Mazama americana pandora*. Its generally brownish color (but not its color pattern), backwardly directed nuchal hairs, and small size misled authors, including myself, into regarding *pandora* as a race of the brown brocket, *Mazama gouazoubira*. Pale brown or *pandora*-like red brockets are common enough as individual color variants or as local constants throughout the range of the species. With few exceptions, the white belly sharply defined from chest and flanks distinguishes *Mazama americana* from *M. gouazoubira*.

Cotton rats and peccaries are among the most viable and vagile of New World mammals. The presence of only one migrant genus (or species) in the upper Pliocene of each continent is not "a whole immigrant fauna" (Patterson, 1937, p. 379) or convincing evidence of an "extensive faunal interchange" (Simpson, 1940, p. 694, footnote 13) *after* closure of the Isthmian gap. Interchange there was, but since the Cretaceous, with the volume and variety directly proportional to the diversity of the faunas, and the population pressures at the intercontinental boundary whether or not a land bridge was present.

The notion that first representatives of most families of northern North American origin crossed a land bridge into South America and radiated there in the Quaternary only, is not compatible with the facts. The tendency has been, however, to reject or ignore the facts incompatible with the notion. Patterson (in Stirton and Gidley, 1949, p. 175) thought it likely that a *Megatherium* from the Bone Valley Middle Pliocene of Florida was an accidental inclusion from overlaying Pleistocene because "the Americas were not united until late Pliocene." In the same work Stirton (loc. cit., footnote) points out that "both megalonychid and mylodontid ground sloths did get through from South America in Hemphillian, Middle Pliocene time." Stirton adds that "no megatheres are recorded in those faunas," but this qualification does not validate Patterson's objection. Thinking along the same line, Patterson (1957, p. 45) regarded the differentiation of a gyropid louse species during Pleistocene as remarkable and the evolution of an anopluran louse genus in the same period as "unlikely" because, "sucking lice [on their mammalian hosts] did not reach South America until the Pleistocene faunal interchange."

Hooper (1949, p. 23) was perhaps the first to recognize the existence of two or more faunal strata among South American immigrants of northern North American origin. His observation that the "*Oryzomys*-like and *Akodon*-like forms" were of an older stratum than that containing *Reithrodontomys* (included *Aporodon*), anticipated his classification of complex-penis-type and simple-penis-type cricetines and my present arrangement of them in South American strata II and V, respectively. Nevertheless, in conforming to the Simpson-Patterson time table, Hooper telescoped the history of these strata into the Pliocene-Pleistocene transition. His conclusion that the differentiation of cricetines in South America was of "a low taxonomic level," somewhat follows Simpson's (1945, p. 207) miscalculated appraisal of South American cricetine evolution. Hooper's estimates have since undergone a radical change (*cf.* Hooper and Musser, 1964a, p. 55, and above, p. 734). My previous (1962, p. 18) hypothesis of the time and sequence of the cricetine invasions of South America was also adjusted to the Simpson-Patterson chronology. It now appears unrealistic and must be discarded.

CONCLUSIONS AND SUMMARY

The evolution of the mammalian fauna of South America began in early Paleocene or late Cretaceous with migrants from Middle America. The first known immigrants were marsupials, condylarths and edentates. Primates

and caviomorph rodents appeared in the Middle Tertiary. Evidently, Tertiary Middle America was a transition zone for mammals passing from North America to South America. More importantly, it was an evolutionary center for mammals of North American extraction and a staging area for successive invasions of northern North America and South America by some of the newly evolved forms. This Middle American fauna must have been rich and flourishing but there are no fossil records of the tropical forest species. The meager middle and late Tertiary records of mammals are of essentially temperate zone pastoral faunas (cf. Olson and McGrew, 1941; Stirton, 1954; Whitmore and Stewart, 1965) which parallel the present temperate zone pastoral fauna of the Mexican and Guatemalan highlands. These faunas no more deny the occurrence of a dominant lowland tropical forest fauna throughout Middle America now than in the past. Correspondingly, the presence of a diversified tropical forest fauna in Tertiary South America demands the existence of an earlier and more primitive tropical forest fauna in Middle America.

Intercontinental faunal exchange at first was a flow from Middle America to South America. With increase in their numbers and diversity some of the newly evolved South American mammals trickled into Middle America by middle Tertiary. By late Tertiary the interchange in kind may have been more or less equal, but on a much larger scale than heretofore. Finally, from late Pliocene onward, the faunal flow from South America to Middle America became the greater, to the extent that the latter is a zoogeographic province of the former (Herskovitz, 1958, p. 806).

The five periods of intercontinental connections, the first in Cretaceous, the last in late Miocene, described by Nygren (1950), may have facilitated the faunal flow for species already on or at the bridge. The intercontinental separations during the intervening periods may have acted as faunal filters but they could never have been barriers comparable in effectiveness to climatic barriers. Virtually all South American mammals, past or present, crossed or could be passed over water gaps such as those which separated the continents during the Tertiary. The crossings must have been continuous with different individuals of the same species crossing at different times and different species of the same genera or families crossing at the same or different times. The volume and rate of mammalian faunal flow at the Isthmus must have always been directly proportional to the diversity of the faunas and their population pressures at the points of interchange.

The last separation between North and South America is the Bolívar geosyncline. This depression formerly extended as a seaway from the Golfo de Urabá in the Caribbean to the Golfo de Guayaquil in the Pacific. Uplift of the Cordillera Occidental and increasing sedimentation reduced the water gap to the Ríos Atrato and San Juan in western Colombia. The Bolívar Trough, nevertheless, still marks the boundary separating many mammalian species, genera, and one family (Geomyidae) of the Middle American Province from the rest of the Neotropical Region.

The late Pliocene-early Pleistocene date generally accepted by zoogeographers for completion of the intercontinental bridge and the beginning of wholesale faunal exchange is not in harmony with the fossil evidence.

Completion of the bridge at whatever date, did not mark the beginning of a rapid and large scale exchange of highly diversified mammalian faunas between Middle and South America. There is slight likelihood that the species and genera of cricetines, canids, procyonids, mustelids, deer, and others could have become peculiarly specialized for isolated niches in South America since the Pleistocene only. The probability is even less that these species and genera invaded South America preadapted for distant and untried habitats and predestined to reach them after trials through hostile environments. The zoological evidence suggests that representatives of all families of northern North American (or Eurasian) origin except those of horses, mastodons, camels, spiny mice, rabbits, shrews and, perhaps, some carnivores (bears, cats), were in South America before the end of the Pliocene. The invasions or, more realistically, the two way traffic, or continental interchange, could have been operative since late Miocene.

South American cricetine rodents are examples of the interchange. Their grade of evolution and the pervasiveness of their adaptive radiation point to long isolation from their North or Middle American ancestors. The history of tropical American cricetines appears in five faunal strata. Stratum I includes the ancestral North and Middle American complex penis stock. Over water migrants from stratum I evolved into the genera and generic groups or tribes of South American stratum II. Some divergent elements of stratum II returned via water routes to Middle and North America and the West Indies. They became the genera, subgenera and species of stratum III. With completion of the land bridge many South American species of stratum II spread overland into Middle America to form stratum IV while two species of a purely North American tribe of simple penis type cricetines invaded South America and became stratum V. There has been little or no change in the taxonomic grade of strata IV and V.

Preliminary analysis of the distribution patterns of a number of other tropical American families with intercontinental range reveals the same or parallel faunal stratifications. As in the case of cricetines, these strata indicate faunal interchange before, during and after completion of the intercontinental land bridge.

NOMENCLATORIAL NOTE

The Family Group Names of New World Cricetine Rodents

The term *Hesperomyini* for New World cricetines is the tribal form proposed by Simpson (1945, p. 83) from the family group name *Hesperomyinae* Murray (1866, p. 358). Neither the family nor tribal name is tenable on nomenclatorial or zoological grounds. Murray's concept of *Hesperomys*, which is the type of his *Hesperomyinae* and Simpson's *Hesperomyini*, is based on twenty North American species, most of them referable to *Peromyscus* and none identical or congeneric with the South American *Hesperomys bimaculatus* Waterhouse, type of the original *Hesperomys* Waterhouse. *Hesperomys* Murray, 1866, therefore, is an invalid homonym of *Hesperomys* Waterhouse, 1839, and unavailable. *Hesperomys* Waterhouse, in turn, has been shown (HersHKovitz, 1962, p.

129) to be a junior synonym of *Calomys* Waterhouse, 1837. Finally, *Calomys* has been treated (op. cit.) as a member of the phyllotine group.

The oldest valid tribal name for New World cricetines is *Sigmodontes* Wagner, 1843 (p. 509). As originally erected, it comprised the genera *Hesperomys* (= *Calomys*), *Reithrodon*, *Holochilus*, *Sigmodon* and *Neotoma*. These taxons were employed in the broadest sense to include all New World species then known. *Sigmodon* Gay and Ord, 1825, the type of *Sigmodontes*, is the oldest generic name for a New World cricetine. Its type, *S. hispidus* Gay and Ord, is cited and diagnosed by Wagner (1843, p. 556). *Sigmodontes* was adopted by a number of authors including Baird (1857, pp. xxvii, 445), Coues (1877, p. 7), Thomas (1897, p. 1019 [Sigmodontinae]), and Gyldenstolpe (1932, p. 1 [sigmodont]). Sigmodontinae as the subfamily name and Sigmodontini as a tribal name are available for New World cricetines and supercede Hesperomyinae and Hesperomyini, respectively. The supergeneric names based on *Sigmodon* which is a complex penis-type-cricetine, apply primarily to sigmodonts in particular and South American cricetines in general. Should North American simple-penis-type cricetines be regarded as tribally distinct, the name Peromyscini is available. More study of New and Old World cricetines, living and extinct, is needed, however, before a relatively stable and generally acceptable classification can be reached. For present purposes, current supergeneric group names used informally are adequate and realistic.

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